
TAXONOMIC REVISION OF
THE CENTRAL AMERICAN
LISIANTHIUS SKINNERI
SPECIES COMPLEX
(GENTIANACEAE)¹

Kenneth J. Sytsma²

ABSTRACT

The *Lisianthus skinneri* (Gentianaceae) species complex consists of six closely related species in Panama. *Lisianthus skinneri* is widespread in Central America at low elevations and is morphologically variable. Five mostly cloud-forest species are endemic to central Panama: *L. jefensis*, *L. peduncularis*, *L. aurantiacus*, *L. habuensis*, and *L. weaveri*. The last three species are described as new. Divergence in floral and vegetative morphology among species is compared and contrasted with genetic divergence (DNA and isozymes) previously presented. Morphological divergence within the species complex is not correlated with molecular divergence.

The *Lisianthus skinneri* (Gentianaceae) species complex is a small, geographically restricted, and interrelated assemblage of taxa. *Lisianthus skinneri* ranges widely throughout Central America but is patchily distributed and shows much ecological and morphological variability. Five endemic species in isolated central Panamanian forests and humid coastal sites exhibit divergence from *L. skinneri* in habit, morphology, breeding system, and ecological tolerance. A taxonomic revision of the *Lisianthus skinneri* species complex based on floral and vegetative morphology is presented here. A biosystematic and evolutionary analysis of the *Lisianthus skinneri* species complex using breeding systems, crossing and cladistic relationships (Sytsma, in prep.), and results of isozyme (Sytsma & Schaal, 1985a) and DNA (Sytsma & Schaal, 1985b) studies is presented elsewhere.

Lisianthus P. Browne is an exclusively neotropical genus in the Gentianaceae. *Lisianthus* and a number of related neotropical shrubby genera form a distinctive but rather diverse group collectively known as the "lisianthioid gentians." *Lisianthus* has been broadly interpreted in the past to include all these lisianthioid genera, usually as *Lisianthus* Linnaeus (1767) or *Lisyanthus* Aublet (1775), orthographic variants of the accepted name

Lisianthus P. Br. (1756) (Taxon 3: 242. 1954). The most comprehensive and recent taxonomic treatment of the Gentianaceae (Gilg, 1895) places *Lisianthus* and *Macrocarpaea* in the tribe Gentianeae, subtribe Tachiinae. The other lisianthioid genera were relegated to the Helieae. The taxonomy of these lisianthioid gentians is in a state of chaos, with only *Lisianthus* (Weaver, 1972) and *Macrocarpaea* (Ewan, 1948; Nilsson, 1968) adequately monographed. A multidisciplinary study is now beginning on these lisianthioid genera (Nilsson, 1970; Maas et al., 1984; Maas, 1985). Many of these genera are confined to poorly accessible high-elevation peaks, thus explaining the small number of available specimens and the poor or incomplete nature of the few existing ones (Sytsma, 1987).

The genus *Lisianthus* consists of 30 species of woody or semiwoody Gentianaceae almost totally confined to Central America and the Greater Antilles. One species, *L. seemannii* (Griseb.) O. Kuntze, ranges into northwestern Colombia. The center of diversity for the genus is in Guatemala and Mexico, which together have 12 species. The genus exhibits a high degree of endemism. Jamaica has eight species, all endemic. Panama has seven species, five of which are endemic. *Lisianthus* species found

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² Botany Department, University of Wisconsin, Madison, Wisconsin 53706, U.S.A.

in Cuba (two species), Hispaniola (one species), and Puerto Rico (one species) are all endemic to each island. Weaver (1972) monographed *Lisianthus* in detail and gave a much needed intrageneric classification scheme. Chromosome numbers for all *Lisianthus* species previously examined (20 out of 30) are identical. Two sections were recognized: *Omphalostigma* and *Lisianthus*. Section *Omphalostigma* (Griseb.) Weaver is composed of only two species, *L. saponarioides* Cham. & Schlecht. and *L. meianthus* Donn. Sm., both exhibiting distinctive salverform corollas and equal filaments inserted near the apex of the corolla tube.

Section *Lisianthus* possesses basically tubular or funnellform corollas and unequal filaments inserted in the lower half of the corolla tube. This section is composed of subsect. *Herbacei* Weaver, annual or perennial suffrutescent herbs with determinate main axes, and subsect. *Fruticosi* Weaver, perennial subshrubs or shrubs with indeterminate main axes. Subsection *Fruticosi* is further divided into three series (*Longifolii* Weaver, *Exserti* Weaver, *Umbellati* Weaver) based on inflorescence architecture, exertion of stamens and styles, and pollen grain reticulation. With its 18 species, series *Longifolii* is the largest species group in the genus and contains the *Lisianthus skinneri* species complex of Panama.

THE *LISIANTHIUS SKINNERI* SPECIES COMPLEX

BIOGEOGRAPHY AND ECOLOGY

Seven species of *Lisianthus* occur in Panama. Four of these already had been known (Elias & Robyns, 1975) and three are described as new in this paper. Of the seven Panamanian species of *Lisianthus*, six (excluding *L. seemannii* (Griseb.) Kuntze) form an unusual and distinctive interrelated species assemblage, hereafter referred to as the *Lisianthus skinneri* species complex. *Lisianthus seemannii*, ranging from Costa Rica to northwestern Colombia, is not especially closely related to the *L. skinneri* species complex, although it is likewise placed in series *Longifolii* of subsect. *Fruticosi*. *Lisianthus seemannii* has much smaller, usually ovate leaves and vegetatively most closely resembles the Jamaican *L. longifolius* rather than members of the *L. skinneri* species complex. The congested inflorescence in *L. seemannii*, a multi-compound dichasium, is unique in series *Longifolii*. The long narrow corolla tube and lobes, paler inside than out, also clearly separate *L. seemannii* from the *L. skinneri* species complex.

Lisianthus skinneri (Hemsley) O. Kuntze is the widest-ranging species in the genus, but with a

marked patchy distribution from southeastern Guatemala to the Darién province of Panama. It occurs from sea level to elevations of near 1,500 m in moist to wet tropical forests. The Atlantic Coastal Plain populations in Guatemala, Honduras, and Panama are frequently situated at sea level, while the populations in Costa Rica and the interior of Panama are found at mid elevations or occasionally higher elevations. *Lisianthus skinneri* has not been collected on the Atlantic Coastal region of Nicaragua or Costa Rica. It is not known whether this absence is due to poor collecting in these areas or whether it reflects an unusual geographic disjunction.

The distribution of *Lisianthus skinneri* is clearly correlated with moisture availability. The mid-elevation forests situated on both the Atlantic and Pacific flanks of the Cordillera de Talamanca extending southeastward from Costa Rica into western Panama and the Cordillera de San Blas and Serranía del Darién in eastern Panama receive abundant rainfall. Only on the more humid and wetter Atlantic side has *L. skinneri* been able to occupy lower elevation sites near or at sea level.

The distribution of *Lisianthus skinneri* throughout its range is markedly patchy, with populations usually separated by many kilometers. This is especially evident in central Panama where large portions of the lower to mid elevations have been extensively explored and collected. *Lisianthus skinneri* is very local in occurrence, as seen in the distribution map of all known populations in Panama (Fig. 1). Some gaps in this distribution will be eliminated with more collecting, especially towards high elevations and on the Atlantic watershed, but undoubtedly the patchy distribution of this species will remain.

Most populations occur in disturbed or partially open habitats. Forest edge sites along roads and paths are now more common because of increasing utilization of the lower elevation forest by people. Often populations are seen in more closed habitats such as tree fall gaps. Scattered groups of individuals are also occasionally encountered in undisturbed forests but do not form the larger clumped populations typically seen in the more disturbed habitats. Population size varies from few to about a hundred individuals. Most populations, however, cover less than 50 square meters and are composed of about 50 flowering shrubs.

In contrast to the wide-ranging distribution of *Lisianthus skinneri*, the other members of the *L. skinneri* species complex are all endemic to central Panama. The physiography of the central Panama mountain system is unusual because it is relatively

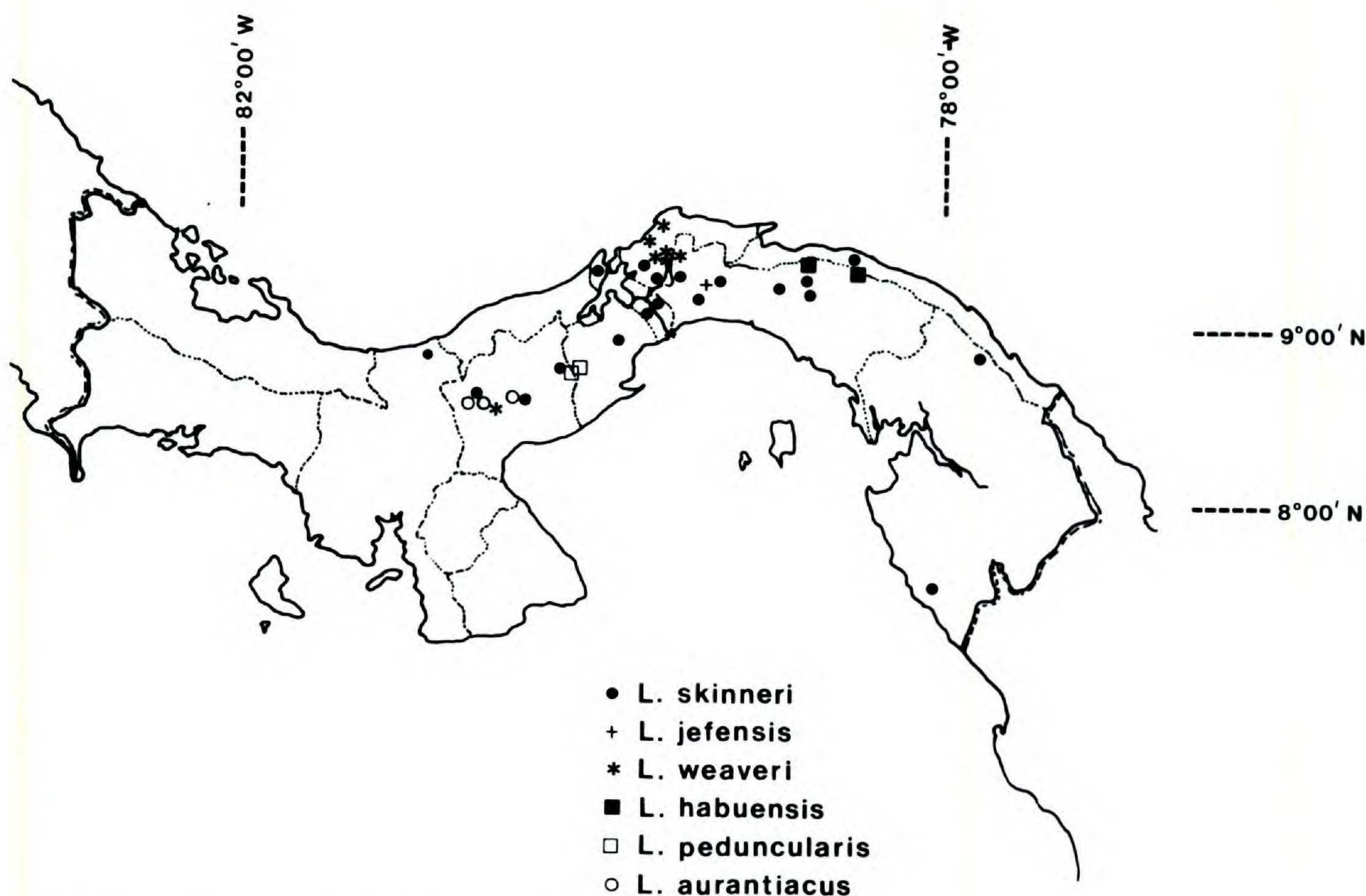


FIGURE 1. Distribution of the *Lisianthus skinneri* species complex in Panama.

low in relief, sinuous in nature, and discontinuous in extent. The central Panama region is thus marked by isolated, cloud forest peaks (600–1,500 m) interrupted by more extensive low- to mid-elevation forests. Four of the additional five species in the *L. skinneri* species complex are restricted to separate cloud forest peaks in this region (Fig. 1). These species include *L. jefensis* Robyns & Elias, *L. peduncularis* L. O. Williams, *L. aurantiacus* sp. nov., and *L. habuensis* sp. nov. *Lisianthus weaveri* sp. nov. is unique in the species complex in that several populations occupy forest-edge sites near beaches on the Atlantic side. Like the cloud-forest populations, these populations still occupy a high-rainfall environment. All species except *L. aurantiacus* and *L. weaveri* are comprised of few populations restricted to a small area. *Lisianthus aurantiacus* and *L. weaveri* are more widespread in distribution but are markedly patchy in occurrence.

MORPHOLOGY

Morphological characters used to delimit species in the *Lisianthus skinneri* species complex are almost exclusively confined to features of the inflorescence and flower. Additional vegetative characters are occasionally divergent in the group and

will also be presented. Only characters that are variable among members of the species complex, and hence of possible phylogenetic interest, will be presented here. A more formal description of all characters will be given in the next section. Measurements were made primarily on dried specimens. Floral characters of the Panamanian populations were measured directly on FAA-preserved material. Only herbarium specimens were examined for populations of *L. skinneri* occurring outside Panama.

Habit. All species except *Lisianthus aurantiacus* are true shrubs. *Lisianthus aurantiacus* in open sites is typically arboreal and can reach heights over 6 m. These trees are slender-stemmed and evenly branched to the top. In more closed forest environments, *L. aurantiacus* is a 2–3 m branched shrub, as are the remaining taxa. Occasionally, taller individuals of *L. peduncularis* are seen in the elfin forest atop Cerro Carocoral. Like most species of sect. *Lisianthus* subsect. *Fruticosi*, these species are not distinctly woody except at the base, even though they persist for years. They usually have a single main stem that is branched above, but totally unbranched flowering plants are seen in *L. skinneri*, *L. weaveri*, and *L. jefensis*. The main shoot has an indeterminate

growth pattern, and the lateral shoots ("flowering branches") have a determinate growth pattern.

Leaves. Two types of leaves are evident in the *Lisianthus skinneri* species complex, true foliage leaves and lateral shoot leaves, which can be a problem if leaf characteristics are used in a systematic analysis. This is especially so because many herbarium collections contain only lateral shoots without true foliage leaves (Weaver, 1972). The foliage leaves of all species except *L. jefensis* are obovate, membranaceous, glossy green above, and paler beneath. Leaves of *L. habuensis* have somewhat undulating margins. *Lisianthus jefensis* leaves are subcoriaceous and usually smaller than those of the other five species. It is interesting that a number of other endemic species on Cerro Jefe also have subcoriaceous to fully coriaceous leaves (pers. obs.). Leaves on the determinate lateral "flowering branches" are smaller, with the transition from foliage leaves to lateral shoot leaves abrupt. Two collections of higher elevation *L. skinneri* from Volcán Arenal, Costa Rica (Wilbur & Stone 10257, Lent et al. 3321) appear to have thickened leaves as well, although Weaver (1972) did not mention it in his monograph. Lateral shoot leaves are ovate to lanceolate and merge into the foliaceous inflorescence bracts. Lateral shoot leaves are absent from *L. aurantiacus* because flowering branches are reduced to single or paired axillary flowers. Small floral bracts are present, however.

Inflorescences. The inflorescence of *Lisianthus* is very difficult to interpret but is an important characteristic in determining phylogenetic relationships within the genus. Architecture of the inflorescence varies considerably in *Lisianthus*, and Weaver (1972) set forth a probable evolutionary scheme for the development of the various types. The arrangement of inflorescences in sect. *Lisianthus* subsect. *Fruticosi* is characterized almost entirely by opposite branching with each division terminated by dichasia. The dichasia are axillary or, more often, both terminal and axillary on determinate lateral shoots. Foliaceous leaves are located below the lowest trichotomy and the upper divisions are subtended by bractlike appendages. The various arrangements of inflorescences in the *L. skinneri* species complex are depicted schematically in Figure 2.

Lisianthus skinneri, *L. weaveri*, and *L. jefensis* are characterized by a ternate compound dichasium in each axillary inflorescence (Fig. 2a). This inflorescence type comes closest in the *L. skinneri* complex to the primitive multi-compound dichasium that Weaver (1972) postulated for the

genus. Simple reduction to a twice-compound dichasium gives the inflorescence type seen in *L. peduncularis* (Fig. 2b). A further reduction of two lateral dichasia (Fig. 2c), or, alternatively, reduction in the terminal dichasium (Fig. 2d) generates the two reduced inflorescences commonly exhibited by *L. habuensis*. Reductions of the *L. peduncularis* type to a single flower, but retaining the three sets of bracts, gives the three-bracted nodes subtending a one-flowered axillary inflorescence sometimes evident in *L. aurantiacus* (Fig. 2e). *Lisianthus aurantiacus*, however, usually has two levels of bracts and either one or two flowers in each axillary inflorescence (Fig. 2f, g).

Calyx. The calyx is variable not only among the species but also within *Lisianthus skinneri*. Populations of *L. skinneri* near sea level in Guatemala and Honduras exhibit the largest calyces in the species. They range from 6 to 8 mm, with the calyx lobes ranging from 3 to 6 mm long. The smallest calyx is seen in populations in the interior of Costa Rica and Panama. Here the calyx ranges from 5 to 6 mm, with the calyx lobes 2 to 4 mm, and is generally appressed and carinate. The calyces in *L. weaveri* are similar to those in *L. skinneri* but are stouter, spreading, and only somewhat ridged. The calyces in *L. peduncularis* and *L. aurantiacus* are very long, 10–13 mm and 13–15 mm, respectively. The calyx lobes of these two species are exceptionally long, averaging about $\frac{3}{4}$ – $\frac{7}{8}$ of the total length. *Lisianthus jefensis* also has a longer, more attenuate calyx than *L. skinneri*. The calyx in *L. habuensis* is similar in size to *L. skinneri* (6–8 mm long) but with longer dark green lobes (4–5 mm long) that are strongly carinate and scarious on the margins.

Corolla. The structure of the corolla in all species is basically uniform (Fig. 3). The basal portion of the corolla enclosing the ovary is constricted into a narrow tube. The stamens are inserted on the inside of the corolla tube at the distal end of the constriction. Immediately above the insertion of the stamens the corolla flares out, often abruptly. Just below the lobes the corolla tube is again constricted, but usually not to the degree as in the basal region. *Lisianthus skinneri* shows extreme variation in the proportions of the corolla. The Guatemalan plants (including the type specimen) have long (5–5.4 cm), narrow, and membranaceous-textured yellow corollas. The corolla lobes are greenish, broad, and short acuminate. Plants from Honduras, Costa Rica, and the interior of Panama closely resemble the Guatemalan plants but have a broader, more inflated corolla tube,

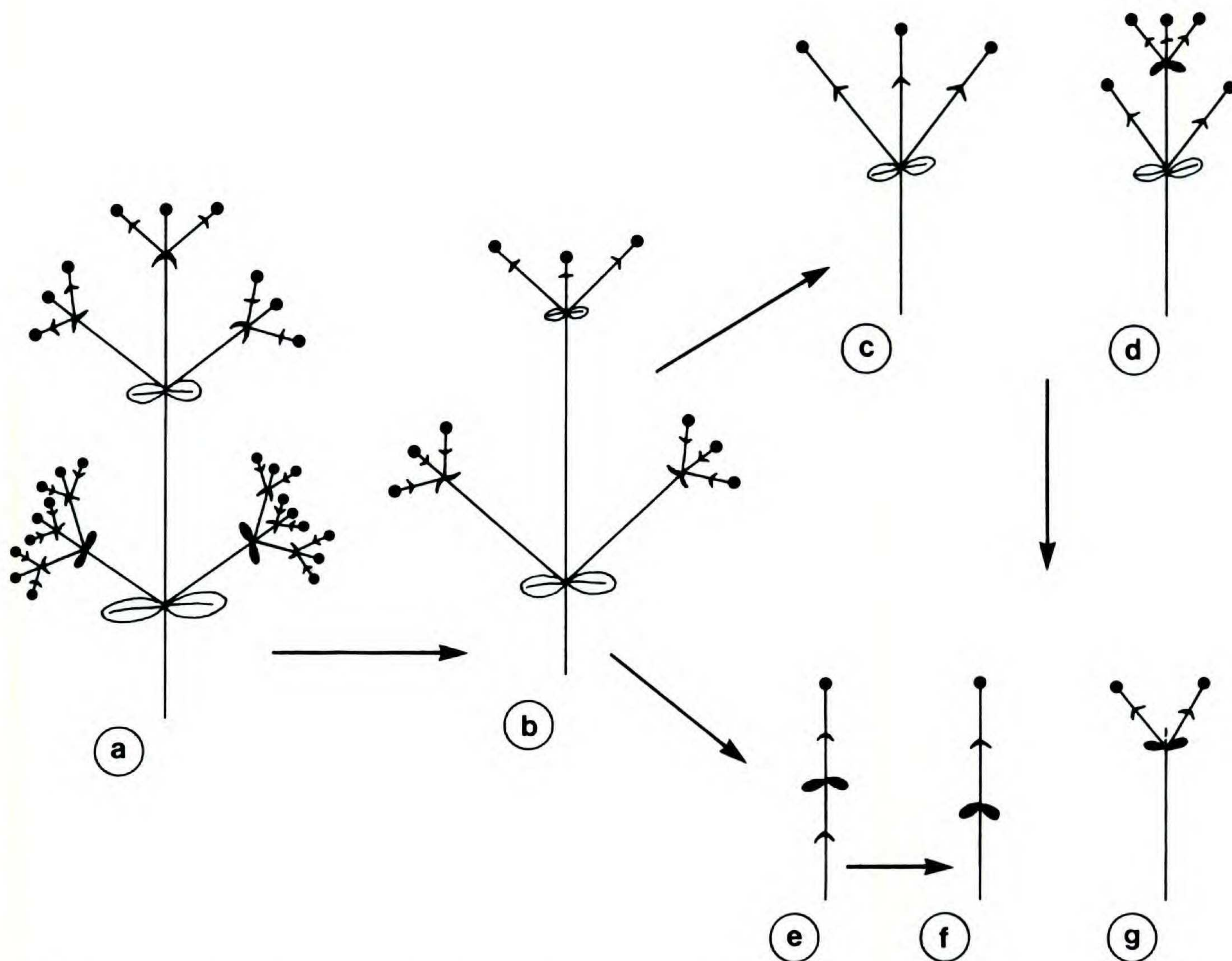


FIGURE 2. Schematic arrangement of the inflorescences in the *Lisianthus skinneri* species complex. Arrows represent probable evolutionary pathways for inflorescence types and do not imply phylogenetic pathways of the representative species.—a. *L. skinneri*, *L. jefensis*, and *L. weaveri*.—b. *L. peduncularis*.—c, d. *L. habuensis*.—e–g. *L. aurantiacus*.

markedly so in the El Llano–Cartí road populations in Panama. The two previously cited Costa Rican collections from Volcán Arenal (*Wilbur & Stone 10257, Lent et al. 3321*) are aberrant in having waxy, thick-textured corollas. The five endemic species in Panama are all characterized by thick-textured, waxy corollas. The correlation of this unique corolla form to wetter higher elevations or to the humid Atlantic Coastal Plain (*Lisianthus weaveri* in part) suggests that this floral character might provide protection against extremely damp conditions and subsequent floral destruction. The high incidence of damaged and rotting, thin-textured flowers on higher-elevation *L. skinneri* plants on Cerro Jefe and the continental divide near Cascajal supports this idea. *Lisianthus jefensis* and *L. weaveri* exhibit the smallest corollas. The corolla of *L. jefensis* is 2.5–4 cm long, with spreading and recurved lobes 4–6.5 mm long, while the corolla of *L. weaveri* is 2.6–4.5 cm long, waxy yellow and green tipped, and surrounds long-exserted styles. The corolla of *L. habuensis* is broad and

4.9–6.1 cm long with the corolla lobes triangular, smallish (3.5–5 mm long and wide at the base), dark green with cream margins, and slightly recurved. The flowers of *L. peduncularis* and *L. aurantiacus* are very similar, both having very long corollas (4.8–6 cm and 5.5–7.8 cm, respectively) and long attenuate lobes (8–10 mm and 9–11 mm, respectively). The pumpkin orange to red corolla color and dark green corolla lobes of *L. aurantiacus* are strikingly different from any Panamanian *Lisianthus*.

Androecium. Weaver (1972) used the placement of stamens as a diagnostic character in separating *Lisianthus skinneri* from *L. jefensis* and *L. peduncularis*. In *L. skinneri* the stamens are inserted well above the apex of the calyx lobes, whereas in the other two species the stamens are inserted at or just above the apex of the lobes. This latter condition also applies to the new cloud-forest species, *L. habuensis* and *L. aurantiacus*. The use of this character as diagnostic is misleading because

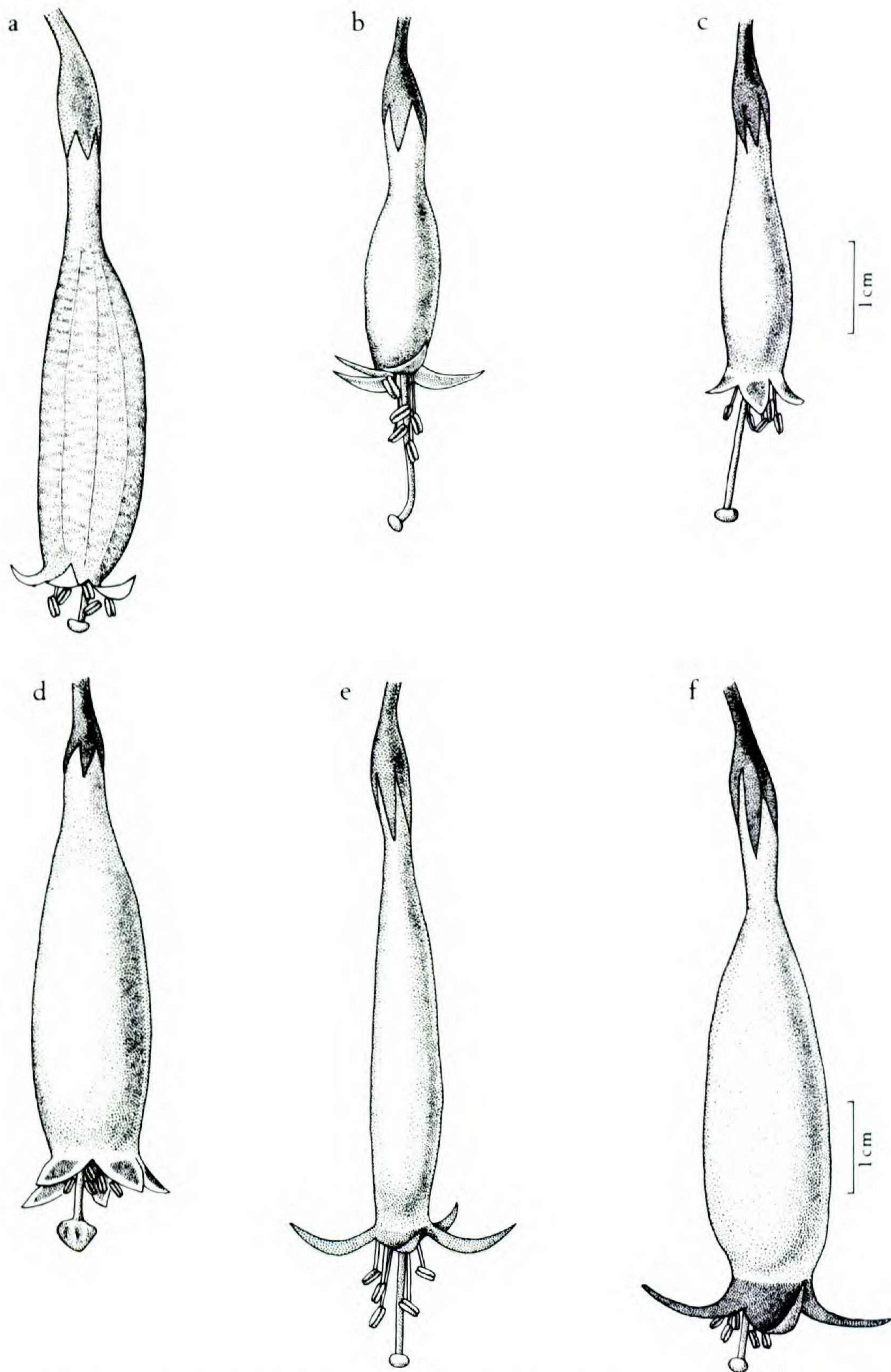


FIGURE 3. Flowers in the *Lisianthus skinneri* species complex.—a. *L. skinneri*.—b. *L. jefensis*.—c. *L. weaveri*.—d. *L. habuensis*.—e. *L. peduncularis*.—f. *L. aurantiacus*.

it does not reflect a difference in the placement of the stamen, but rather in the length of the calyx. All species in the *L. skinneri* species complex have the stamens attached to the inner corolla tube about the level of the apex of the ovary. Stamen length varies depending on corolla tube length, with most species having stamens protruding slightly from the corolla lobes. The stamens in *L. jefensis* are proportionally longer than in the other species and are conspicuously exerted. Anthers and pollen are

whitish yellow in most *L. skinneri* individuals, greenish yellow in some individuals of *L. skinneri* and in the other species, except for *L. aurantiacus*, in which they are bluish green.

Gynoecium. Style, ovary, capsule, and seed size, like the stamens, are correlated with flower size in general. Exceptions include *Lisianthus jefensis* and *L. weaveri*, which both have longer exerted styles. Stigma shape and size are diag-

nostic characters separating out *L. habuensis*. All other species in the complex exhibit smooth, small stigmas (1–1.5 mm broad). The stigma in *L. habuensis* is unique and divergent in being large (2.5–3 mm broad), conical, and rough textured.

SYSTEMATIC TREATMENT

The grouping of populations into formal taxonomic categories has two underlying purposes. The first and traditionally the primary purpose of such an endeavor is the construction of an information retrieval system that permits effective communication about the populations (Raven, 1979). The taxonomic system constructed should preserve information that enters the system and should minimize its loss once taxonomic decisions have been made. The second purpose is the construction of a taxonomic system that best reflects the phylogenetic or historical relationships of the populations. Often, both goals of taxonomic decision-making cannot be simultaneously satisfied.

In delimiting species in the *Lisianthus skinneri* species complex, problems were encountered in grouping populations into formal categories of "species." As previously indicated, DNA techniques indicated the paraphyletic nature of *L. skinneri* (Sytsma & Schaal, 1985b). Populations of *L. skinneri* examined at the DNA level could be placed in two separate lineages that have been involved in separate speciation events. Cladistic analysis strictly following Hennig's (1966) principles would raise a western Panamanian *L. skinneri* population

to the species level to preserve monophyly and to reflect better the apparent phylogeny of the species complex. This separation is unsatisfactory because it violates the first purpose of an effective information retrieval system. Although clearly this western population is *phylogenetically* divergent by DNA analysis, it also clearly falls within the range of morphological variation of the widespread *L. skinneri* as predefined. Because of the broad distribution and ancestral nature of *L. skinneri*, it is very likely that many clusters of populations in *L. skinneri* will be shown by DNA analysis to represent divergent and independent lineages and by similar reasoning would also have to be accorded species status.

In assigning formal names to clusters of populations in the *Lisianthus skinneri* species complex, therefore, additional sources of data were used in addition to genealogical or phylogenetic interpretation. For example, *L. jefensis* is identical to an eastern population of *L. skinneri* by cladistic DNA analysis (Sytsma & Schaal, 1985b) but is maintained as a distinct species derived from *L. skinneri* based on its peculiar morphology, lack of hybridization, and endemic nature. The western Panamanian population of *Lisianthus skinneri*, apparently a member of a lineage that has given rise to other species, is maintained as *L. skinneri* because no changes in morphology, reproductive barriers, or habitat preference are outside the range of variation found in typical members of *L. skinneri*.

KEY TO THE LISIANTHIUS SKINNERI SPECIES COMPLEX

- 1a. Leaves subcoriaceous; anthers and styles conspicuously exerted, and long surpassing the corolla lobes; endemic to Cerro Jefe, Panama 3. *Lisianthus jefensis*
- 1b. Leaves membranaceous; anthers and styles included, or slightly exerted and not conspicuously surpassing the corolla lobes, or only the styles conspicuously exerted.
 - 2a. Corolla lobes \geq 7 mm long; calyx lobes \geq 6 mm long.
 - 3a. Inflorescence of 1–2 axillary flowers; corolla pumpkin orange to red; plant often treelike 6. *Lisianthus aurantiacus*
 - 3b. Inflorescence of twice compound dichasia; corolla yellow; plants shrubby 5. *Lisianthus peduncularis*
 - 2b. Corolla lobes \leq 5 mm long; calyx lobes \leq 6 mm long.
 - 4a. Calyx lobes 4–5 mm long; inflorescence of simple dichasia, never ternately compound; stigma 2.5–3 mm in diameter, conical, convoluted 4. *Lisianthus habuensis*
 - 4b. Calyx lobes 2–4 (rarely 5) mm long; inflorescence of twice or ternately compound dichasia; stigma 1–1.5 mm in diameter, rounded, smooth.
 - 5a. Corollas 5–5.4 cm long, thin-textured; styles slightly exerted past anthers 1. *Lisianthus skinneri*
 - 5b. Corollas 2.6–4.5 cm long, thick-textured; styles long exerted past anthers 2. *Lisianthus weaveri*

1. ***Lisianthus skinneri*** (Hemsley) O. Kuntze, Rev. Gen. Pl. 2: 429. 1891. *Leianthus skinneri* Hemsley, Biol. Centr. Amer. 2: 345. 1882. *L. skinneri* (Hemsley) Perkins, Bot. Jahrb. (Syst.) 31: 492. 1902. TYPE: Guate-

mala. Locality not given: *Skinner s.n.* (lectotype, K, photographs, F, MO).

Lisianthus arcuatus Perkins, Bot. Jahrb. Syst. 31: 492. 1902. TYPE: none designated.

Lisianthus scopulinus Robyns & Elias, Ann. Missouri

Bot. Gard. 55: 62, fig. 2. 1968. TYPE: Panama. Veraguas: mouth of Río Concepción, *Lewis, Croat & Hawker 2799* (MO).

Shrub or subshrub, 0.5–3 m tall; stem terete, erect, green. Leaves membranaceous, deep to light green, paler below; blades 4–24 cm long and to 7.7 cm wide, obovate to obovate-elliptic, sharply acuminate; the costa prominent, lateral veins 2–3, ascending; petiole amplexicaul, winged. Inflorescences terminal or axillary, composed of ternately compound, laxly flowered dichasia; foliaceous leaved below first division, bracted above; bracts opposite, lanceolate to linear, 2 mm long or longer. Flowers horizontal to nodding; calyx 5–7 mm long, the lobes 3–5 mm long, carinate dorsally, \pm scariously margined, stout or attenuate, appressed or spreading; corolla tubular-funnelform, constricted apically and distally, the tube 5–5.4 cm long and to 1 cm broad, bright yellow, occasionally greenish-tipped, membranaceous, the lobes ovate, 2.5–5.5 mm long, 2.5–4 mm wide, yellowish green to dark green, often with cream margins, often recurved at tip, short to long acuminate. Stamens inserted within corolla at apex of ovary; filaments 4.2–4.7 cm long, unequal in length, longest one at least equaling or surpassing corolla lobes; anthers 2–3 mm long and ca. 1 mm wide, bilobate at the base; pollen whitish yellow. Style 4.7–5.1 cm long, usually slightly exerted past anthers; stigma peltate, 1–1.5 mm broad. Capsules fusiform, 1.8–2.2 cm long, beaked by persistent style to 9 mm long; seeds asymmetrical, surface corrugated, to 0.75 mm long. Chromosome number, $n = 18$.

Distribution. From sea level to 1,300 m in moist to wet tropical forests or roadsides, at middle elevations in Costa Rica and the interior of Panama, and along the Atlantic Coastal Plain of Guatemala, Honduras, and Panama.

Lisianthus skinneri as delimited here encompasses all populations of the *L. skinneri* species complex outside Panama and most populations at low to mid elevations in Panama. Based on distribution and DNA analysis, *L. skinneri* is the ancestral species in the complex (Sytsma & Schaal, 1985b). The four endemic cloud-forest species that were examined by DNA analysis arose from at least two lineages within *L. skinneri*. The corolla is longer and thinner in texture (membranaceous) than corollas in the now segregated *L. weaveri*. The latter species has smaller flowers with thickened and waxy corollas like other species in this complex. *Lisianthus skinneri* as defined here is composed of populations showing moderate vari-

ability (Weaver, 1972). This is not surprising, considering both the widespread distribution and ancestral nature of the species. This variation, however, presents considerable problems when species circumscription is attempted. *Lisianthus scopulinus* Robyns & Elias from Veraguas Province, Panama, has somewhat large calyx lobes (4–5 mm long) for *L. skinneri*. It resembles *L. skinneri* in all other traits and is here merged with *L. skinneri* as another geographically variable population. One population of *L. skinneri* from Costa Rica is unique in having thickened flowers and in occurring at higher elevations on Volcán Arenal (*Wilbur & Stone 10257*, *Lent et al. 3321*). This population was not visited during the study, so its status as a distinct element in the *L. skinneri* species complex is only tentative.

Representative specimens examined. GUATEMALA. IZABAL: south shore of Lake Izabal, *Proctor et al. 3049* (F). ALTA VERA PAZ: eastern portions of Vera Paz & Chiquimula, *Watson 380a* (G). HONDURAS. ATLANTIDA: 42 km SE of Tela to La Ceiba, *Davidse & Pohl 2194* (MO); San Alejo, *Standley 7829* (F); Cuyamel, *Carleton 584* (F). COSTA RICA. ALAJUELA: 17–22 km beyond San Ramón to Cataratas, *Almeda et al. 4301* (F, MO); middle slopes N side of Volcán Arenal, *Lent 3868* (F, MO); *Lent et al. 3321* (F); Villa Quesada near San Carlos, *Smith 1884* (F, MO); 13.5 mi. E of Arenal, 6.5 mi. W of Fortuna, *Wilbur & Stone 10257* (DUKE, F, MO, NY, US). GUANACASTE: Volcán Miravalles, *Burger & Gentry 9126* (F); Hacienda Santamaria, *Dodge et al. 6320* (F, MO); lower slopes Cerro La Giganta [Cerro Miravalles], 2 km W of Río Naranjo, *Utley & Utley 1899* (DUKE); Tilarán, *Valerio 115* (F); SE lower slopes Volcán Miravalles, *Wilbur & Almeda 16623* (DUKE, F, MO, US). HEREDIA: Finca Hnos. Vargas, Puerto Viejo de Sarapiquí, *Jiménez 3577* (MO); Río La Paz & Cariblanco de Sarapiquí, *Pittier 14159* (US). PANAMA. COCLÉ: La Mesa, N of El Valle de Antón, *Allen 2369* (MO); continental divide past Llano Grande, *Dressler 5627* (MO); Río San Juan below junction with Río Tífe, *Hammel 3436* (MO); 5 mi. past Llano Grande near continental divide, *Sytsma 3872* (MO); 4 mi. past Llano Grande at continental divide, *Sytsma 3939* (MO); 9 km N of Llano Grande, *Hammel 1713* (MO). COMARCA DE SAN BLAS: El Llano–Cartí Rd., 10 km N of Panamerican Hwy., *Folsom 2622* (MO); Nusagandi, along El Llano–Cartí Rd., below (N of) Punta Mamá, 350 m, *de Nevers & Nuñez 3565* (MO); Río Nergala, 100–300 m, *de Nevers & Herrera 4548* (MO); Río Irgandí and Río Cartí Senni, *de Nevers & Herrera 6610* (MO, WIS); Río Cangandí & Río Titamibe, 50–150 m, *de Nevers 4677* (MO); Río Sidro, base of Cerro Habu, *Sytsma et al. 2622* (MO); Cerro Habu, 400–800 ft., *Sytsma et al. 2799* (MO). DARIÉN: upper Río Membrillo on construction road to San Blas, *Duke 10891* (MO). PANAMÁ: Cerro Campana, near FSU Field Station, ca. 800 m, *Kennedy & Williams 233* (WIS); Cerro Jefe region [Cerro Azul & Altos de Pacora], *Antonio 3204* (MO); *Correa et al. 582* (DUKE, MO); *D'Arcy et al. 3955* (MO); *Dwyer 2649, 9445* (MO); *Knapp 927* (MO); *Lewis et al. 2314* (MO); *Maas et al. 1540* (MO); *Sytsma & D'Arcy 3672, 3673* (MO); *Sytsma & Antonio 3828* (MO); *Sytsma & Knapp 4795* (MO); *Sytsma et al. 5006*



Lisianthus weaveri

FIGURE 4. *Lisianthus weaveri* (Antonio 3737 (MO)).—a. Habit.—b. Flower.—c. Dehisced fruit.

(MO); Tyson 5320 (DUKE, MO); Weaver & Foster 1482 (DUKE, MO, NY); Weaver & Wilbur 2242 (DUKE, NY), 2244 (DUKE, MO, NY); Webster et al. 16475 (DUKE, MO); Wilbur et al. 11338, 15540 (DUKE); Wilbur & Teeri 13606 (DUKE, MO, NY); El Llano-Cartí region, 6–8 mi. from Pan American Highway, An-

tonio 1690 (MO); Croat 49099 (MO); D'Arcy 10591 (DUKE, MO); Folsom 1439 (MO); Gentry 5788 (MO); Hahn 324 (MO); Hamilton & Stockwell 1102 (MO); Hammel 862 (MO); Kennedy et al. 3148 (MO); Knapp 930 (MO); Mori et al. 4719 (MO); Mori & Kallunki 5565 (MO); Nee & Dressler 9327 (MO); Sytsma &

Sytsma 3099 (MO); *Sytsma* 3989 (MO); *Sytsma & Andersson* 4432 (MO); *Wilbur & Luteyn* 19490 (DUKE, F, MO, NY); 11 km N of Gamboa, *Croat* 32937 (MO); Río Boquerón, trail to Río Pequeni, *Dressler* 6001 (MO); 10 km N of Magarita on road to Madroño, *Hammel & D'Arcy* 5117 (MO); *Hammel* 6007 (MO); headwaters Río Arenal, *Johnston* 1502 (MO); Gorgas Memorial Labs yellow fever research camp, Río Piedras, *Mori & Kalunki* 3364 (MO); Pipeline road, 9 km N of Gamboa, *Nee* 7681 (MO, WIS); Pipeline road, 8 km N of Gamboa, *Nee* 9580 (MO); Canal Zone, Río Indio, *Steyermark & Allen* 17427 (MO). VERAGUAS: mouth of Río Concepción, *Lewis et al.* 2799 (DUKE, MO).

2. *Lisianthus weaveri* K. J. Sytsma, sp. nov.

TYPE: Panama. Colón: Santa Rita ridge trail along Río Piedras, 8,000 ft., 9 Mar. 1979, *Hammel* 6357 (holotype, MO; isotype, WIS). Figure 4.

Frutex ad 2.5 m altus. Folia obovata-elliptica, ad 23 cm longa et 8.5 cm lata. Inflorescentiae axillares et terminales, dichasio biternato vel triternato. Calyx 5–6 mm longis; tubus ad 2 mm longus; lobi 3–4.5 mm longi, scariosescens ad margineum. Corolla aurea, cerea, 2–3.5 cm longa; lobi triangulares, virides, cerescens ad margineum, 2–3 mm longi et lati. Stamina filamentis \pm exsertis. Stilus antherae superans 5–10 mm; stigma peltatum, 1–1.5 mm latum. Capsulae fusiformes ad fusiformes late, 1.5–2 cm longa.

Shrub or subshrub, to 2.5 m tall; stem terete, erect, green. Leaves membranaceous, deep green above, paler below; blades to 23 cm long and to 8.5 cm wide; obovate to obovate-elliptic, \pm strongly acuminate tipped; the costa prominent, with 2–3 sets of lateral veins, these ascending and becoming parallel with margin; petiole amplexicaul. Inflorescences terminal or axillary in upper nodes; ternately compound dichasia (or only twice compound); foliaceous leaved below, bracted above. Flowers horizontal or nodding; calyx 5–6 mm long, tube to 2 mm long, the lobes 3–4.5 mm long, carinate dorsally, scariously margined, triangular-attenuate, \pm appressed; corolla tubular-funnel-form, constricted distally and \pm apically, the tube 2.2–3.3 cm long and to 8 mm wide, waxy and fleshy, bright yellow; lobes 2–3 mm long and wide, broadly triangular, green but with cream or yellow margins. Stamens inserted within corolla at apex of ovary; filaments to 2.5 cm long, equaling or barely exceeding corolla lobes; anthers 2–2.5 mm long and 0.75–1 mm wide, bilobate at base, pollen yellowish. Style to 3.5 cm long, far exserted (5–10 mm) past anthers; stigma peltate, 1–1.5 mm broad. Capsules fusiform to broadly fusiform, 1.5–2 cm long, beaked by persistent style to 10 mm long.

Distribution. *Lisianthus weaveri* is known from mid- to high-elevation cloud forests in Coclé

and Colón provinces and at sea level on the Atlantic Coastal Plain in Colón Province, Panama.

Lisianthus weaveri is the only cloud forest species of *Lisianthus* found on both sides of the the Panama Canal. This species has been collected from a number of sites in the higher ridges leading to Cerro Bruja, so far an inaccessible peak dominating the ridge of mountains paralleling the Atlantic Ocean in eastern Colón Province. Populations of *L. skinneri* collected in the lower reaches of this region are quite distinct from those of *L. weaveri*. *Lisianthus weaveri* is also found near the continental divide above El Cope, Coclé Province, the southeastern edge of the Cordillera de Talamanca extending northwestward towards Costa Rica. Three additional populations occupy high-rainfall, forest-edge sites near the beach on the humid Atlantic side of Panama. *Lisianthus weaveri* resembles *L. jefensis*, also with short and waxy corollas, but lacks the exserted stamens and coriaceous leaves of the latter. The short, fleshy, and waxy corolla and the exserted style readily distinguish *L. weaveri* from lower-elevation *L. skinneri* populations. Weaver (1972) cited the *Weaver & Wilbur* 2249 collection as distinctive with its short, fleshy corolla and long exserted style. Although *L. skinneri* is certainly variable in floral features, the collections of *L. weaveri* surpass this level of variability and can be readily distinguishable from all other collections of *L. skinneri*. A possible but as yet untested origin of *L. weaveri* might involve hybridization between *L. skinneri* and *L. jefensis*. In many of its floral characters, *L. weaveri* is strikingly intermediate between these geographically adjacent species. *Lisianthus weaveri* is named in honor for Richard E. Weaver, Jr., monographer of the genus.

Representative specimens examined. PANAMA. COCLÉ: Alto de Calvario, *Folsom & Jaslon* 2680 (MO); El Cope, W of sawmill, *Hammel* 3545 (MO). COLÓN: Cerro Pilón, *Loften* s.n. (MO); Cerro Santa Rita, *Allen & Allen* 5104 (MO); Santa Rita trail to Río Piedras, *Antonio* 3737, 3869 (MO, WIS); Río Miguel de La Borda near Guasimo, *Croat* 9919 (MO); W of Portobello, *D'Arcy & D'Arcy* 6698 (F, MO); Maria Chiquita, *Dwyer & Kirkbride* 7771 (DUKE, MO); S approach to Cerro Bruja from Río Escandaloso, *Hammel* 3210 (MO); Río Boquerón and Río Escandaloso, *Hammel* 3988 (MO, WIS); Santa Rita hills, *Smith & Smith* 3434 (F); 3 km SW of Río Guancho, road between Puerto Pilón and Portobelo, *Sytsma & Andersson* 4792 (MO); 5–7 mi. SE of Portobelo, *Weaver & Wilbur* 2249 (DUKE, F, MO, NY); Santa Rita ridge, *Wilbur et al.* 15020 (DUKE).

3. *Lisianthus jefensis* Robyns & Elias, Ann. Missouri Bot. Gard. 55: 60, fig. 1. 1968 (as "*Lisianthus*"). TYPE: Panama. Panamá: Cerro Jefe, *Elias & Hayden* 1798 (MO).

Slender shrub or subshrub, 1–2.5 m tall; stem terete, green. Leaves glossy dark green above, paler below; blades to 12 cm long and to 4.5 cm wide, subcoriaceous, oblanceolate to narrowly obovate, apically acuminate, the lateral veins prominent; petioles amplexicaul, winged. Inflorescences terminal or axillary, composed of twice to ternately compound dichasia, rarely reduced, usually loosely arranged; bracts opposite, 2–5 mm long. Flowers horizontal, or more often nodding; calyx 7–13 mm long, lobes long acuminate, 5–9 mm long, scariously margined, weakly carinate; corolla tubular, thickened and waxy, constricted apically and distally, tube 2.1–3.5 cm long, sometimes greenish tipped, lobes 4–6 mm long, triangular, to 3 mm wide. Stamens inserted on corolla at apex of ovary; filaments 1.5–3 cm long, the longest ones long exserted past corolla lobes; anthers 2.5–3.5 mm long, yellow, bilobate at base. Style to 3.5 cm long, conspicuously exserted past anthers; stigma pelate, to 1 mm broad. Capsule shortly fusiform, 1–1.6 cm long, beaked; seeds asymmetrical, corrugated. Chromosome number, $n = 18$.

Distribution. *Lisianthus jefensis* is known only from the Cerro Jefe region of the Province of Panamá, elevation 800–900 m. This species is widespread near the rounded peak but can be found scattered at lower elevations. Cerro Jefe is subjected to alternating periods of wet cloud cover and intense sunlight due to an unusual combination of local topography and climate. *Lisianthus jefensis* is a conspicuous and locally widespread member of the floristically diverse and predominantly shrubby flora of Cerro Jefe that contains numerous other local endemics. This forest is dominated by species of *Clusia* and *Calopthrinax cookii*.

Two populations of *Lisianthus skinneri* are found immediately below the cloud forest zone. The transition between the two life zones is abrupt, with the change readily perceived. In one locality individuals of *L. skinneri* and *L. jefensis* are only meters apart, with no hybrids reported or seen (see also Weaver, 1972). DNA analysis clearly indicates that *L. jefensis* has been derived recently from eastern populations of *L. skinneri*. *Lisianthus jefensis* is morphologically similar to *L. weaveri* in floral characters and might have been involved in the origin of the latter species by hybridization with *L. skinneri*.

Representative specimens examined. PANAMA. PANAMÁ: Cerro Jefe, 6–8 mi. past Goofy Lake, 3–4 mi. past Cerro Azul, 800–900 m elevation; *Almeda & Nakai* 3452 (F, MO); *Antonio et al.* 3402 (MO); *Antonio* 4699 (MO); *Busey* 798 (MO); *Correa & Dressler* 1154 (MO,

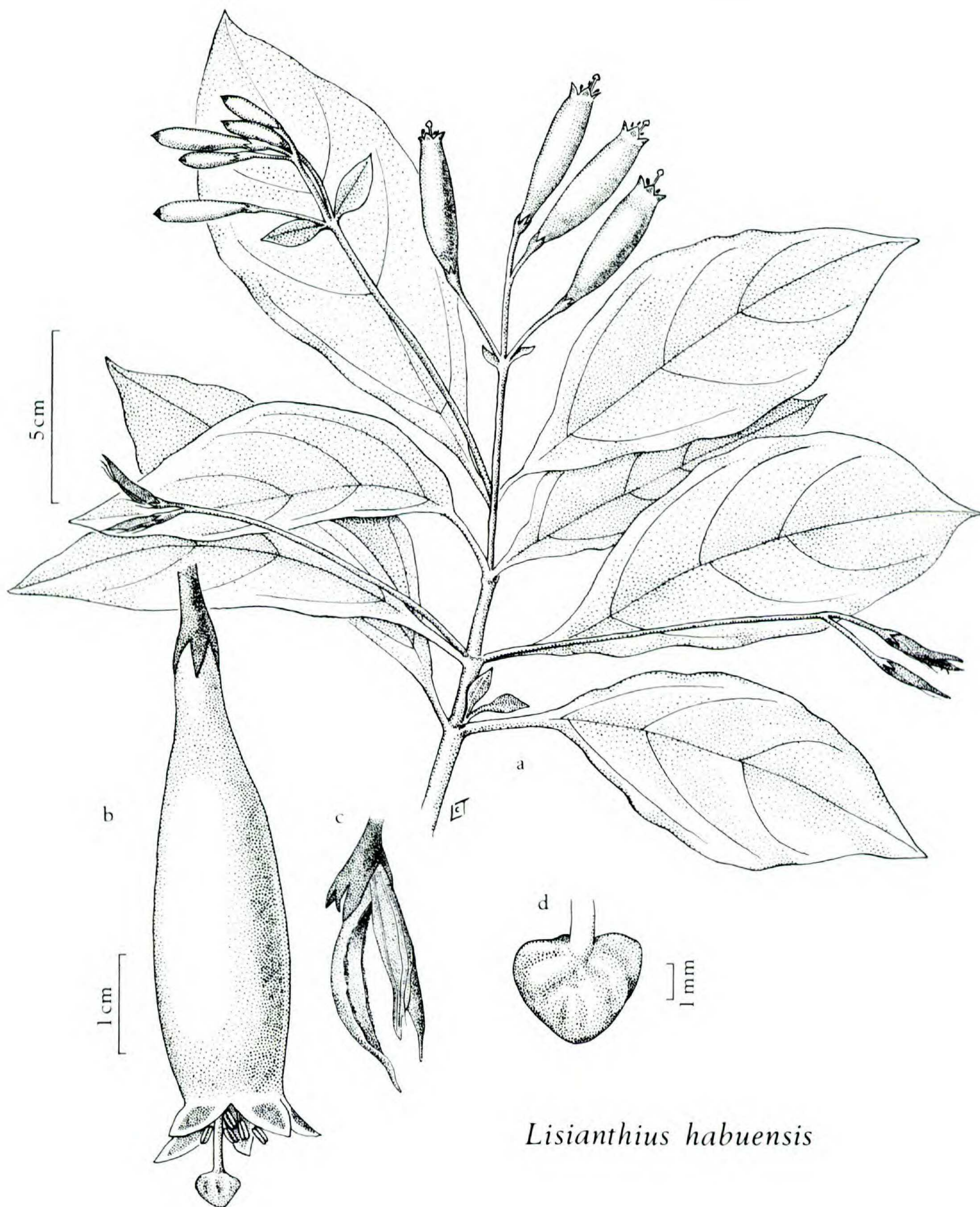
NY); *Correa et al.* 1617 (DUKE, MO); *Croat* 14435, 17341 (MO); *D'Arcy & Hamilton* 14801 (MO); *D'Arcy et al.* 15516 (MO); *Duke* 8010 (MO), 9413 (MO, US); *Dwyer et al.* 5035 (MO); *Dwyer & Hayden* 8087 (MO); *Folsom et al.* 5655 (MO); *Foster* 1164 (DUKE); *Gentry* 2115 (DUKE, F, MO), 6771 (F, MO); *Hammel* 3716, 4817 (MO); *Hamilton & D'Arcy* 602 (MO); *Hayden* 1008 (DUKE, MO); *Kirkbride & Crebbs* 16 (F, MO); *Knapp* 925, 2225, 3509, 3538, 5202 (MO); *Luteyn* 3200 (DUKE, F, MO); *Luteyn & Kennedy* 3959 (DUKE); *McPherson* 6878 (MO); *Miller & Miller* 896 (MO, WIS); *Mori & Kallunki* 2376 (MO, US); *Mori* 7129 (MO); *Nee* 11456 (MO); *Robyns* 4438 (MO); *Skog et al.* 4219 (MO, US); *Stimson* 5390 (DUKE); *Sullivan* 218 (MO); *Sytsma* 1399, 2025 (MO); *Sytsma et al.* 2902 (MO); *Sytsma & Antonio* 3829 (MO); *Sytsma & D'Arcy* 3695, 3696 (MO); *Sytsma & Knapp* 4798, 4799 (MO); *Sytsma* 4105 (MO); *Tyson et al.* 3203 (MO); *van der Werff & van Herdeveld* 6972 (MO, WIS); *Weaver & Foster* 1481 (DUKE, MO); *Weaver & Wilbur* 2241, 2243, 2250 (DUKE, F, MO, NY, US); *Webster et al.* 16457 (DUKE, MO); *Wilbur & Teeri* 13604 (DUKE, MO, NY); *Wilbur et al.* 15524 (DUKE, F, MO, NY, US); *Wilbur* 24126 (DUKE, F); *Witherspoon & Witherspoon* 8484 (US).

4. *Lisianthus habuensis* K. J. Sytsma, sp. nov.

TYPE: Panama. Comarca de San Blas: Cerro Habu, vicinity of peak, cloud forest, 800 m, 78°49'W, 9°23'N, *Sytsma, Antonio & Dressler* 2685 (holotype, MO). Figure 5.

Frutex 1–4 m altus. Folia obovata-elliptica, 13–19.5 cm longa, 3.5–5.8 cm lata. Inflorescentiae axillares et terminales, dichasio reducto, 3–7-floribus; pedunculis elongatis. Calyx viridis, tubularis, 6–8 mm longis; lobi 4–5 mm longi. Corolla aurea, cerea, 4.9–6.1 cm longa; lobi triangulares, virides, cerescens ad margineum, 3.5–5 mm longi et lati. Stamina filamentis ± exsertis. Stilus antherae superans 1–3 mm; stigma grande, conicum, corrugatum, ad 3–3.5 mm longa. Capsulae fusiformes, ad 2 cm longa.

Shrub or subshrub, 1–4 m tall; stem terete, erect. Leaves membranaceous, usually pale green to green; petiole 1.3–2.5 cm long, amplexicaul; blade obovate to obovate-elliptic, basally attenuate, apically long acuminate to attenuate, 13–19.5 cm long and 3.5–5.8 cm wide, with 2–4 ascending lateral veins, the costa prominent beneath. Inflorescences of reduced dichasia, usually once compound, or reduced, on long axillary or terminal peduncles, 14–30 cm long; bracts opposite, over 2 mm long. Flowers nodding; calyx tubular, green, 6–8 mm long, the lobes lanceolate, acuminate, scariously margined, strongly carinate, 4–5 mm long; corolla bright yellow, waxy, the tube funnel-form, inflated, 4.9–6.1 cm long, the lobes dark green with yellow border, broadly deltoid or triangular ovate, 3.5–5 mm long and broad, recurved slightly. Stamens inserted within corolla tube at apex of ovary; filaments exserted just past corolla lobes; anthers 2–3 mm long, bilobate at base; pollen



Lisianthus habuensis

FIGURE 5. *Lisianthus habuensis* (Sytsma et al. 2685 (MO)).—a. Habit.—b. Flower.—c. Dehiscent fruit.—d. Stigma.

yellowish. Style surpassing anthers; stigma large, conical, to 3.5 mm long, contorted, almost corrugated. Capsule fusiform, to 2 cm long, with short beak; seeds asymmetrical, seed texture corrugated.

Distribution. *Lisianthus habuensis* occurs near the eastern range of the species complex in the province of Panamá and in the Comarca de

San Blas. A large population was discovered at the very top of Cerro Habu (800 m), Comarca de San Blas. This peak is located on the Cordillera de San Blas adjacent to the Atlantic coast and receives extremely abundant rainfall. *Lisianthus habuensis* dominates the shrub layer on the very tip of Cerro Habu but is not found more than 50 m below

the summit. A second population was found near the Continental Divide on the the road from El Llano to Cartí, Province of Panamá, approximately 20 km from Cerro Habu. A large portion of this population grows on the roadside, with a few scattered individuals in the forest interior. Several populations of *L. skinneri* are located 3–5 km south of (below) *L. habuensis* along the El Llano–Cartí road. A third population was discovered at the headwaters of three rivers in the Province of Panamá at elevations of 100–400 m.

Lisianthus habuensis is distinct from all other species of *Lisianthus* by having an unusual stigma. The large ovoid stigma is obvious in the field, although not as noticeable on dried herbarium specimens. The unique corolla and lobes further distinguish it from all other species. DNA evidence indicates that this species is most closely related to a lineage giving rise to *L. peduncularis* and *L. aurantiacus*.

Additional specimens examined. PANAMA. PANAMÁ: headwaters of Río Chagres, Río Esperanza and Río Piedras, 79°20'W, 9°20'N, *de Nevers 4086* (MO); 8 mi. along El Llano–Cartí road from Pan American Highway, 300–400 m, *Sytsma 4002* (MO, WIS); *Sytsma et al. 5003* (MO, WIS).

5. *Lisianthus peduncularis* L. O. Williams, *Fieldiana, Bot.* 31: 408, fig. 1. 1968 (as "*Lisianthus*"). TYPE: Panama. Coclé: El Valle de Antón, *Allen 3410* (MO).

Shrub or subshrub, occasionally large, to 3.5 m tall; stems terete, distinctly woody below, herbaceous above. Leaves petiolate, the petiole amplexicaul; blades dark green above, paler below, 6–20 cm long, to 7.5 cm broad, broadly ovate, abruptly acuminate to acute; the lateral veins prominent, strongly ascending. Inflorescences longly pedunculate, loose and open, once compound dichasia, sometimes reduced; bracts opposite, lanceolate to sublinear. Flowers nodding, the pedicels 6–13 mm long. Calyx 7.5–13 mm long, the lobes lanceolate, carinate, scariously margined, long acuminate at the apex, 5.5–10 mm long. Corolla tube funnel-form, 4.5–6 cm long, bright yellow, inflated in the middle; the lobes dark green, 6–10 mm long, long acuminate, usually spreading. Stamens inserted in the corolla tube at the apex of the ovary; filaments 3.2–4 cm long, just surpassing the corolla tube but not the lobes; anthers 2–3 mm long, yellow, bilobed at the base. Style to 5 cm long, just exceeding the corolla lobes, always surpassing the anthers; stigma peltate. Capsule fusiform, to 1.5 cm long, sharply beaked; seeds irregular in shape, corrugated in texture. Chromosome number, $n = 18$.

Distribution. *Lisianthus peduncularis*, endemic to the north rim and adjacent ridges of El Valle de Antón, Coclé Province, is now known to be composed of three small populations. Two populations are restricted to exposed elfin forest ridges (900–1,000 m) and usually are found associated with *Symbolanthus pulcherrimus* Gilg, a lisianthoid shrub characteristic of such habitats. A third population is found on the northern lower flanks of the El Valle crater (800 m). This large population of approximately 80 individuals grows on a soft porous rhyolite bedrock in association with a low *Clusia*-dominated scrubby open forest similar to the vegetation type on Cerro Jefe. *Lisianthus skinneri* has been collected on the road from El Valle leading up to these *L. peduncularis* sites. P. Allen (2369) collected it in 1941, but the species has not been collected since from the region despite extensive searches and collecting through the Flora of Panama project.

Morphologically, *Lisianthus peduncularis* most closely resembles the new *L. aurantiacus* with which it shares long corolla tubes and lobes, and reduced inflorescences. They differ strikingly in habit and corolla color. Both occur at the western edge of the species complex in Panama. DNA analysis clearly indicates that these two species form a close pair of "sister species."

Representative specimens examined. PANAMA. COCLÉ: N rim, El Valle de Antón, *Allen 1793* (MO, US); La Mesa, N of El Valle, *Allen 2369* (US); Cerro Pajita, *Allen & Allen 4187* (MO); El Valle, Club Campestre, *Croat 14288* (F, MO); Cerro Pilón, *Croat 22945* (DUKE, F, MO, WIS); Cerro Pilón, *Duke 12192* (MO); Cerro Carocoral, *Duke & Dwyer 15094* (MO); Cerro Carocoral, *Kirkbride 1094* (MO); trail past La Mesa, *Clusia* forest, *Luteyn 4082* (DUKE); Cerro Pilón, *Mori 6631* (MO); Cerro Gaital, *Reveal & Balogh 4945* (MO); Divide SW of La Mesa at end of logging road, *Stein & Hamilton 1002* (MO, WIS); Cerro Carocoral, *Sytsma 3815* (MO); Las Minas, N of El Valle, *Sytsma 4039* (MO); La Mesa, N of El Valle, *Sytsma et al. 4367* (MO); inside crater at El Valle de Antón at La Mesa, *Weaver et al. 2247* (DUKE, F, NY, US); trail to La Mesa, 4.5 mi. past El Valle, *Wilbur & Luteyn 11696* (DUKE, MO, NY); trail past La Mesa, *Clusia* thicket, *Wilbur et al. 15622* (DUKE).

6. *Lisianthus aurantiacus* K. J. Sytsma, sp. nov. TYPE: Panama. Coclé: Mountains between La Pintada and Cascajal, *Dressler 5625* (holotype, MO; isotype, WIS). Figure 6.

Frutex vel arbor, ad 6.5 m alta; truncus ad 7 cm latis, ramosis aequaliter apicem versus. Folia obovata-elliptica, ad 25 cm longa et 6.5 cm lata. Inflorescentiae axillares, dichasio reducto, 1–2-floribus; pedunculis elongatis, ad 12 cm longis. Calyx viridis, tubularis, 10–16 mm longis; lobi 8–13 mm longi, acuminati longe. Corolla aurea, au-



Lisianthus aurantiacus

FIGURE 6. *Lisianthus aurantiacus* (Hammel 2508 (MO)).—*a*. Habit.—*b*. Flower.—*c*. Dehiscent fruit.

aurantiacus, 5.5–7.8 cm longa; lobi triangulares, virides, 10–14(–17) mm longi, 3–5 mm lati. Stamina filamentis ± exsertis; antherae 2.5–5 mm longae. Stilus antherae superans 1–3 mm; stigma peltatum, aquamarinum. Capsulae fusiformes, 1.8–2.5 cm longa.

Shrub or slender-trunked tree, to 6.5 m tall. Stem to 7 cm wide, terete, evenly branched to the top. Leaves petiolate, the petiole 5–15 mm long, amplexicaul; blade glossy dark green above, slightly paler below, 2–3 lateral veins conspicuous, strongly ascending, the costa prominent below, membranaceous; to 25 cm long and 6.5 cm broad, obovate to obovate-elliptic, basally cuneate to slightly attenuate, apically acuminate. Inflorescence axillary, opposite, consisting of 1 or 2 flowers; the peduncles to 12 cm long, containing 1–3 sets of foliaceous to linear bracts, the larger bracts to 15 mm long; the pedicels to 2 cm long. Flowers strongly nodding. Calyx tubular, dark green, 10–16 mm long, the lobes lanceolate, long acuminate, scariously margined, carinate at the base only, 8–13 mm long. Corolla 5.5–7.8 cm long, tubular-funnelform, inflated, the tube bright pumpkin orange, the lower $\frac{1}{2}$ narrowly constricted, the lobes dark green, triangular, acuminate and spreading, 10–14(–17) mm long and 3–5 mm wide at the base. Stamens 4.5–6.3 cm long, exserted to the midpoint of the lobes; filaments filiform, inserted on the corolla tube at the apex of the ovary; anthers 2.5–5 mm long, slightly sagittate at base, yellow. Style 4.7–6.7 mm long, slightly exserted past the anthers; stigma blue-green, capitate, slightly bilobed at apex. Capsule fusiform, 1.8–2.5 cm long, 5–7 mm diam., with a beak 4 mm long.

Distribution. *Lisianthus aurantiacus* has the most widespread distribution of the cloud-forest species. It has been collected in three localities: on the continental divide near Cascajal, Coclé Province (650 m); below the continental divide on the Atlantic watershed north of El Cope, Coclé Province (800–900 m); and the Cerro Tífe region 15 km west of El Cope (400–450 m). *Lisianthus aurantiacus* usually occurs sporadically in closed forests, with only a few individuals seen together. Populations in the more disturbed Cascajal area are large and more treelike (to 6 m), effectively forming a canopy. *Lisianthus aurantiacus* is found at lower elevations than the other cloud-forest species. The cloud forests in this region of Coclé Province are lower in elevation than in other areas of central Panama because of local climatic conditions. The forests are floristically more similar to mid-elevation moist forests where *L. skinneri* thrives. Indeed, a population of *L. skinneri* was

discovered growing sympatrically with *L. aurantiacus* in the Cascajal area.

Lisianthus aurantiacus is undoubtedly the most spectacular member of the genus. Its arboreal habit, very large pumpkin orange corolla (thus the specific epithet), and highly reduced inflorescence distinguish it from all other *Lisianthus* species. A more northern species, *L. axillaris*, is strikingly similar to *L. aurantiacus*. The only species with red or orange flowers known prior to *L. aurantiacus* was *Lisianthus axillaris*, a common roadside plant in Belize and surrounding regions. It exhibits not only a reddish corolla, but also an axillary inflorescence of a single flower as well. This is a clear case of floral convergence. *Lisianthus aurantiacus* is most closely related to *L. peduncularis*, with which it shares several other floral characters.

Representative specimens examined. PANAMA. COCLÉ: trail from Caño Sucio to Cerro Tífe, base of waterfall, *Antonio* 3687 (MO, WIS); area between Caño Blanco del Norte, Caño Sucio and Chorro del Río Tífe, *Davidse & Hamilton* 23581 (MO, WIS); Caribbean side of divide at El Cope, *Hamilton & Davidse* 2680, 2693 (MO, WIS); 7 km N Llano Grande, road to Coclesito, *Hammel* 1970, 2508 (MO, WIS); continental divide N of Penonomé, road to Coclesito, *Hammel* 4032 (MO); continental divide N. of Penonomé, between Llano Grande and Cascajal, *Hammel* 7221 (MO, WIS); *Hammel & Kress* 8509 (DUKE); S of Cascajal, Continental Divide, *Knapp* 1954 (MO, WIS); waterfall of Río Tífe, *Knapp* 3704 (MO, WIS); Los Pedregales, ridge between Río Blanco del Norte and Río Caño Sucio, *Knapp & Dressler* 3788 (MO, WIS); Coclecito Rd., Continental Divide, 500 m, *de Nevers et al.* 6726 (MO, WIS); between Caño Sucio and Cerro Tífe, *Sytsma et al.* 2532 (MO, WIS); 4 mi. past Llano Grande to Cascajal, *Sytsma* 3981 (MO, WIS); *Sytsma et al.* 4379, 5005 (MO, WIS).

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